

A PHYLOGENETIC SERIES OF THE CALIFORNIA CLOSED-CONE PINES SUGGESTED BY THE FOSSIL RECORD

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During the course of extended studies in the fossil record, in an attempt to trace the origin and migration of the forest associations of California and to explain the highly endemic nature of the flora, many interesting things have been brought to light. Outstanding among these is an unusually long series of fossil cones of the species of closed-cone pines now inhabiting the coastal and insular regions of California. This series runs from the present through the Recent and Pleistocene, and well down toward the base of the Pliocene. Altogether over three hundred such cones have been taken, and in many instances they are accompanied by wood, fascicles of needles, staminate catkins, pollen and seeds. In a group with a morphological structure pointing to close inter-relationship, such a series of plant remains from the fossil record ought to suggest something as to the nature of this relationship.

The term "closed-cone pine" is locally applied to those species of hard pines whose cones are persistent for long periods on the tree and frequently remain closed for several years after maturity. It is not uncommon to find the cones still persistent, only a few feet from the ground, on the trunk of a one hundred foot tree. Such cones may have been produced thirty-five or forty years before. Most frequently, however, five to ten years would represent the average duration of the cones on the trees. There are at present four rather polymorphic species with two recognized varieties, which by no means give a proper concept of the variation within the group. In addition to these there are two marked forms, now presumably extinct, described from the fossil record. A discussion of these species, fossil and living, follows.

PINUS MASONI Dorf. Figure 4

The earliest record of these pines was taken from the lower Pliocene where they occur in the Merced sandstones near San Francisco and in the Pico shales near Ventura, California. Another poorly preserved cone was taken from the Pliocene Santa Clara lake beds on Coal Mine Ridge near Palo Alto¹. This Pliocene material, though closely resembling the modern *Pinus muricata* Don, has been given the name *Pinus Masoni* by Dorf,² and varies from the modern form in having the scales of one side of the cone consistently produced into a triangular attenuate beak. It falls within the range of the extremes of variation of the modern *Pinus muricata*, though by no means can it be said that this extreme of variation characterizes the modern species. What records are available to us indicate that *Pinus Masoni* was essentially of this type throughout its entire range during the Pliocene. It seems to have been a part of an insular forest growing during Plio-

MADROÑO, vol. 2, pp. 49-56. Feb. 25, 1932.

¹Scott, F. M., Bull. Torr. Bot. Club, 1927.

²Dorf, Erling, Pliocene Floras of California. Carn. Inst. Wash. Pub. 412, 1930.

cene time on islands that extended from what is now central California to southern California. In the southern locality there was, in association with this species, another pine that has been called *Pinus Pieperi* by Dorf and has been referred to *Pinus sabiniana* of the modern floras. In the northern localities the pine is in association with *Pseudotsuga* which is well represented by cones and wood. In studies of the Pliocene floras of California no other traces of species of closed-cone pines were found. The record as we now know it suggests this form as ancestral to the modern closed-cone pines.

PINUS LINGUIFORMIS Mason sp. nov. fos. Figure 5

Cone 10 cm. long by 5 cm. wide³, ovoid, attenuate, asymmetrical, apparently reflexed on the branch; scales on the outer side produced to a long flattened tongue-like beak 8 to 12 mm. long by 6 mm. wide, tipped by a stout prickle, of which our specimen shows only a portion remaining.

Locality. "From a layer of black clay between 800 and 900 feet at the 'Los Alamitos pump station' of the Long Beach Water Works about one-half mile northeast of Signal Hill in Los Angeles County. The layers of clay are thin (five to twenty inches), separated by thick layers of sand and fine gravel."⁴

Collection. Univ. Calif. Coll. Pal. Bot. no. 446.

This cone was sent in by Mr. Catey, engineer for the Long Beach Water Works. Superficially it resembles an attenuate form of the "*Pinus Masoni*-*Pinus muricata*" complex, but is more massive and has a much fewer number of produced scales per cone. This is characteristic of the smaller-coned species. The tongue-like character of these scales, also, is not found in the other species group. Probably the material from the La Brea asphalt beds, in part at least, may be referred to this species. Such disposition, however, needs confirmation by re-study of the specimens now deposited in the Los Angeles Museum. The cone figured by Mason in "*Fossil Records of Some West American Conifers*" (Plate 3, Fig. 1), is a little too massive to be referred to *Pinus muricata* and more probably should be referred to *Pinus linguiformis*.

Pinus linguiformis clearly shows relationship to the Pliocene *Pinus Masoni*, but with respect to its attenuate habit and the reduction in the number of prolonged scales, as well as in the massiveness of these scales, it suggests a marked tendency toward the modern *Pinus attenuata* Lemmon.

³The specimen is very much flattened and the figures refer to the width of the fossil cone. Correction for this flattening gives the cone a diameter of only 32 mm. at its thickest point. It must be borne in mind also, that in the preservation of plant remains of this sort a marked shrinkage occurs. This shrinkage sometimes amounts to as much as 25% in the drying of the specimen. These facts necessarily alter the concept of the species as it naturally grew.

⁴Transmitted by letter of November 10, 1930, from Mr. Catey.

We know little as to the habitat of *Pinus linguiformis* unless, as has been suggested, it is specifically identical with material in the La Brea deposits. Here we have a small-leaved form of *Quercus agrifolia*, a thick-seeded form of *Juniperus Californicus*, *Sambucus glauca*, *Celtis reticulata*, *Xanthium* sp., and *Juglans Californica*. As suggested by this association the habitat was considerably drier than the present habitat of *Pinus muricata* but is not out of keeping with that of *Pinus attenuata*.

PINUS MURICATA Don. Figure 3

Of all the coastal species of closed-cone pines, *Pinus muricata* is the most widespread and apparently the most successful. It runs through a great range of variation in morphological detail as well as in adaptation to habitat. The most extreme variation occurs in the cones, particularly with regard to the shape of the processes on the scales, which ranges from slightly pyramidal to an elongate cylindro-conical structure. Sometimes they are straight and sometimes recurved; usually they are tipped by a prickle. The more typical form of the cone scale of the modern species is a broad pyramidal, somewhat recurved umbo, tipped with a usually persistent prickle. The cones range from 3 to 8 cm. in length. A small "thimble-cone" form is found on Santa Cruz Island. The habitat range is equally impressive. The literature repeatedly refers to *Pinus muricata* as a "swamp pine". This is far from being the general truth. It is true that along the Sonoma and Mendocino county coasts there occur marshes and poorly drained areas in which *Pinus muricata* grows, but it likewise grows on the hill slopes and, in some cases, on hilltops where drainage is rapid. Much of the Inverness Ridge region is of this type. The largest and best developed trees here are on well-drained rotten Montara granite. Likewise at Monterey they grow on granitic soil that is well drained.

The distribution of *Pinus muricata* is of particular interest. It occupies a narrow, highly discontinuous strip along the coast from the vicinity of Trinidad Head in Humboldt County to La Purissima Ridge in Santa Barbara County, thence southward in Insular California to Guadalupe and Cedrus islands, and again on the mainland of Baja California at Point San Quentin, where it has been described as *Pinus muricata* var. *Anthonyi* Lemmon, a form of rather doubtful taxonomic rank.

During Pleistocene time *Pinus muricata* appears always to have been associated with *Pinus radiata*, and it seems evident from the nature of the fossil record that *Pinus radiata* was the dominant species of the two. Today we find them associated in only two very local spots, one on Huckleberry Hill at Monterey and the other near the northern boundary of San Luis Obispo County.

The species has been found in the fossil record from Lower Pleistocene through the Recent. The cones at Carpinteria⁵, which number

⁵Chaney and Mason, Science, n. ser., vol. 76, no. 1702, p. 156.

over 50, fall well within the range of variation of the modern species but have a more pronounced development of the scales, as is indicated in the illustration in figure 3. At Millerton in Marin County, seven cones of *Pinus muricata* have been taken, all of which compare more favorably with the typical form of today as it grows on Inverness Ridge in Marin County. At Tom's Point, near the entrance of Tomales Bay, three cones of this species have been taken which conform exactly with those from the contemporaneous Millerton beds. There seems no doubt that this large and variable species has been on the ascendancy since Pliocene time, where it appears as *Pinus Masoni*. It then goes through a great variation during the Pleistocene and finally emerges during the Recent, as a highly plastic and successful species, which from all indications is on its way toward an even greater multiplicity of habitat forms. These, if given a chance by man, will probably before another geologic epoch greatly increase the numbers of closed-cone pines.

PINUS REMORATA Mason⁶. Figure 1

The Santa Cruz Island pine is a very characteristic small-coned pine with the cones ovoid in shape and ranging from symmetrical to only slightly asymmetrical. Some of them show a slight swelling on the umbos. Most of them stand at right angles to the stem. The needles are in fascicles of two and are rather heavy. They contain from twelve to eighteen resin ducts. Today this pine is confined to some of the islands of Alta and Baja California. In the past we have records of its occurrence on Santa Cruz Island⁷ as well as in the asphalt deposits at Carpinteria on the adjacent mainland. In its morphology as well as its aspect this pine is clearly related to *Pinus muricata*, but certainly is a step toward the other insular endemic, *Pinus radiata* var. *binata* Engelm. of Guadalupe Island. It seems evident that *Pinus remorata* was differentiated prior to middle Pleistocene and has persisted on the islands. Apparently it is not a successful invader. The presence of remains of the northern elephant with the fossils in the Pleistocene has been used to indicate a continental connection of what are now islands to the mainland. In spite of the connection this pine, at least in view of present information, has not been able to migrate and to establish itself on the present continent. All of the fossils in hand are very symmetrical and do not range over 6 cm. in length.

PINUS RADIATA Don. Figure 2

Pinus radiata, the Monterey Pine, is perhaps the most widely known of the closed-cone-pines. It is very variable in the shape of the cone and in the extent of development of the scales, a fact which has resulted in an extensive synonymy in botanical literature. In general, the species has three needles to a fascicle, although some trees will

⁶Mason, H. L., Madroño, vol. 2, p. 8, 1930.

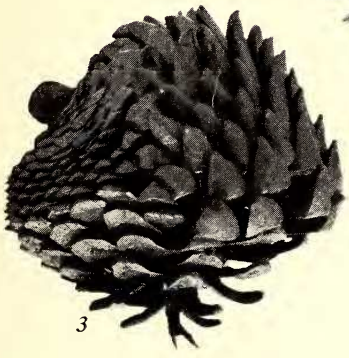
⁷Chaney and Mason, Carn. Inst. Wash. Pub. 415, 1930.



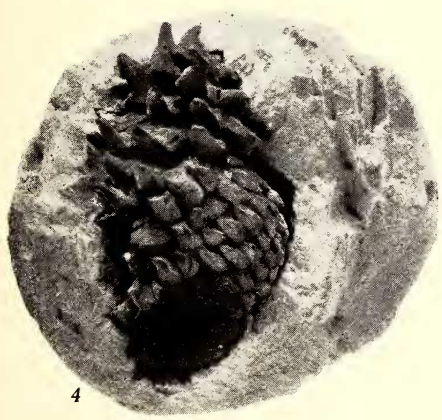
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1. PINUS REMORATA Mason. 2. P. RADIATA Don. 3. P. MURICATA Don. 4. P. MASONI Dorf. 5. P. LINGUIFORMIS Mason. See "Explanation of Plate," p. 56.

show as high as thirty per cent of the needles in fascicles of two, and occasionally trees are found with needles in fascicles of four and five⁸. The umbos or the enlarged scales of the cone are usually rounded, sometimes somewhat angular or quadrate. The cone is usually broadly ovoid in form and asymmetrical in outline. Considerable variation in the size of the cone occurs also. In general, there is a marked average increase in size observable as one moves southward in its range, although there is also much local variation.

The species ranges discontinuously on the mainland of California from near Ano Nuevo Point on the San Mateo-Santa Cruz County line to the vicinity of Moro Rock in San Luis Obispo County. It occurs again in typical form on Guadalupe Island⁹ two hundred miles off the coast of northern Baja California along with *Pinus radiata* var. *binata* Engelm. The latter is characterized by having a predominant number of needles in fascicles of two, as well as by having slightly smaller cones which tend to vary toward *Pinus remorata* Mason.

The fossil records of *Pinus radiata* are particularly interesting because of the former extension of range indicated and because of the evolutionary aspects of the foliage suggested. The southernmost record thus far taken is from the asphalt deposits at Carpinteria, where it is associated with *Pinus muricata* and *Cupressus goveniana* as well as with several species of *Arctostaphylos* and one of *Ceanothus*. The cones are large and well formed in a manner suggestive of those of the southern part of the modern range. In the habitat they outnumber the cones of *Pinus muricata* considerably, yet in the fascicles of needles that are so abundant in the deposit there is a marked preponderance of 2-needle fascicles. They outnumber the 3-needle fascicles about eight to one. Proceeding northward we find *Pinus radiata* again in a gravelly clay deposit at Mussel Rock south of San Francisco, where it is associated with *Pseudotsuga*, and again at Millerton and at Tom's Point on Tomales Bay. The Millerton locality is of particular interest because it occurs on the edge of a forest of *Pinus muricata* and contains an overwhelming preponderance of fossil *Pinus radiata*. Here a series of over two hundred cones have been taken, of which only seven are *Pinus muricata*. Although the deposit at Tom's Point is not so rich as that at Millerton, the preponderance of cones of *Pinus radiata* here also is well marked.

No record has as yet been taken that can be cited definitely as *Pinus radiata* var. *binata* Engelm. However, the overwhelming preponderance of 2-needle fascicles in the Pleistocene deposit at Carpinteria would suggest that in the development of this species the 2-needle phase was, at that time, far more important than at present and possibly was ancestral to the 3-needle phase.

⁸Haasis, F. W., *Madroño*, vol. 2. p. 29, 1931.

⁹The writer wishes to express his appreciation to Mr. J. T. Howell and to the California Academy of Sciences for the use of notes and material obtained on a recent trip to Guadalupe Island, where the occurrence of typical *Pinus radiata* Don in the living flora was definitely established.